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ORIGINAL PAPER

Using dendrochronology to model hemlock woolly adelgid effects on eastern hemlock growth and vulnerability

James Rentch · Mary Ann Fajvan · Richard A. Evans · Brad Onken

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Abstract This study examined the relationship between eastern hemlock (*Tsuga canadensis* (L.) Carr.) crown condition and changes in radial growth associated with infestation by hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae) (HWA). Tree-ring chronologies of eastern hemlock were used to develop a binomial decline index based on three consecutive years of below average growth. Radial growth decline was modeled, using logistic regression, as a function of an extensive array of tree, crown, and site variables that were collected over an 11 year period in Delaware Water Gap National Recreation Area. Some site-related variables such as site-location and aspect were significantly related to decline probabilities when considered individually. However, the total proportion of response variance accounted for was low, and the only site variable included in the final model was mean plot-level HWA infestation level. For every 1% increase in mean percent HWA infestation per plot, there was an 8% increase in the likelihood that a tree would be classified as being in decline. Tree crown variables such as live crown ratio, crown density, and the modified ZB_{adj} index, a combination of foliage transparency and branch dieback, had the most explanatory power, both individually and in the final model. These crown variables were relatively accurate predictors of the degree of hemlock growth decline during HWA infestation.

J. Rentch
Division of Forestry and Natural Resources,
West Virginia University, P.O. Box 6125, Morgantown,
WV 26506-6125, USA
e-mail: jrentch2@wvu.edu

M. A. Fajvan (✉)
Northern Research Station, USDA Forest Service,
180 Canfield St., Morgantown, WV 26505, USA
e-mail: mfajvan@fs.fed.us

R. A. Evans
Delaware Water Gap National Recreation Area, National
Park Service, 294 Old Milford Rd., Milford, PA 18337,
USA
e-mail: richard_evans@nps.gov

B. Onken
USDA Forest Service State & Private Forestry,
Northeastern Area, 180 Canfield Street, Morgantown,
WV 26505, USA
e-mail: bonken@fs.fed.us

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Introduction

Hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae) (HWA) is a non-native invasive insect that feeds on eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*T. caroliniana* Engelm.). HWA is currently established in 17 eastern states, covering approximately 50% of eastern hemlock's range (http://www.na.fs.fed.us/fhp/hwa/maps/hwa_2006.pdf), and is causing tree decline and wide-ranging mortality effects. Hemlock mortality associated with HWA establishment can range from almost none to 95% (Bair 2002; Mayer et al. 2002; Orwig and Foster 1998). Mortality can occur quickly and uniformly throughout a stand, especially in the presence of other stressors, or can occur slowly and in patches for more than a decade (Eschtruth et al. 2006).

HWA is bivoltine, and reproduces parthenogenetically. Unlike most insects, HWA feeds, grows, and reproduces during the winter. Colder winter temperatures can cause HWA mortality and hinder population establishment and growth (Parker et al. 1998; Shields and Cheah 2005), and are believed to slow spread rates (Evans and Gregoire 2007). HWA is spreading to new areas at a rate of 15.6 km/year south of Pennsylvania and 8.13 km/year (or less) in the northern portion of hemlock's range (Evans and Gregoire 2007).

Hemlock woolly adelgids insert long stylet bundles into the underside of the base of needles, and feed on the stored nutrients in the parenchyma cells of xylem rays (Shields et al. 1996). High densities of HWA deplete food reserves and diminish the ability of a tree to produce new growth (Evans 2002). Further injury may result from injection of toxic saliva during feeding (McClure 1991). Subsequent needle discoloration, premature needle drop, branch tip dieback, and foliage thinning, can result in tree mortality in 4–15+ years (McClure 2001; Mayer et al. 2002; Orwig 2002).

HWA is chronic in nature. Unlike other defoliating forest insects (e.g., gypsy moth and hemlock looper), where impacts are immediately obvious, the effects of HWA typically become apparent a year or more after infestation. Eastern hemlock has not exhibited resistance to HWA, and native predators have not been effective at controlling HWA populations (Montgomery and Lyon 1996; Wallace and Hain 2002). Introduced biocontrol agents have shown promise but have yet to be proven effective in HWA control (McClure 2001; Reardon and Onken 2004). The wide range in the rate of eastern hemlock decline and mortality from HWA infestations suggest that tree and site variables influence hemlock's vulnerability to HWA feeding (Pontius et al. 2002). Identifying which of these variables have the strongest effects could be used to predict vulnerability of different hemlock trees and stands to HWA. Management efforts could then focus on environmental manipulations to prolong survivability until effective biocontrols are in place.

Eastern hemlock's vulnerability to HWA

Eastern hemlock is the most shade tolerant tree species in the eastern United States and typically is found in understory canopy positions as well as in sub-dominant overstory positions. Hemlocks grow slowly even when young and at high densities can survive in repressed conditions for hundreds of years (Godman and Lancaster 1990). Hemlocks growing in slope positions and aspects with adequate and consistent moisture generally survive an HWA infestation longer than trees growing on droughty sites and southern aspects, or waterlogged sites (Sivaramakrishnan and Berlyn 2000; Mayer et al. 2002; Orwig 2002; Pontius et al. 2002).

Bonneau et al. (1999, 2000) proposed a matrix of site characteristics to differentiate health classes of hemlock, and found that hemlock health significantly correlated with slope position, aspect, hydrology group, maximum depth to bedrock, soil order and texture, and drainage class. However, two other studies found that site characteristics explained a relatively small amount of the total variation in vegetation change (Royle and Lathrop 2000), and elevation and distance to streams showed a modest relationship with defoliation (Young and Morton 2002). Comparing two sites in the Delaware Water Gap National Recreation Area (DEWA), Eschtruth et al. (2006) found no significant differences in hemlock decline in relation to topographic positions or distance from streams.

Hemlocks in dominant and codominant overstory crown class positions appear to survive HWA longer than intermediate and overtopped crown class trees (Onken 1996; Orwig and Foster 1998; Eschtruth et al. 2006). Trees that receive less sunlight in lower canopy positions (Smith et al. 1997) probably have less extensive root systems, higher root competition, lower stem capacitance, and insufficient carbohydrate reserves. Trees that have slower radial growth prior to infestation may also be more susceptible to severe infestation and die sooner (Davis et al. 2007). Loss of foliage from HWA feeding also can increase vulnerability. Mayer et al. (2002) proposed that when hemlock feeding reduced foliar transparency to a threshold value of 60%, significant mortality quickly followed.

Hemlock's diameter growth response to HWA may also vary according to the magnitude and duration of crown feeding. Radial growth patterns provide a means for detecting and reconstructing tree decline for both individual trees and populations (McClenahen 1995). Because the population dynamics of HWA infestation are difficult to measure, identifying and dating changes in radial growth patterns can be used to reconstruct infestation history (Davis et al. 2007) and establish relationships with tree and stand variables that also affect diameter growth rate. Several techniques are used to reconstruct tree and stand disturbance histories by determining whether radial growth showed significant growth decreases (Fajvan and Seymour 1993) or growth increases (reviewed in Fraver and White 2005) associated with disturbance events. These methods require the establishment of a threshold response, beneath or beyond which a given event is deemed a valid growth decrease or increase. These thresholds are biologically and mathematically derived but require some level of subjectivity for determining appropriate levels for a given research objective.

The objective of this study is to use dendrochronological information to determine which site and tree factors best predict the vulnerability of hemlocks to HWA. Specifically, we developed a radial growth response model using site factors, tree characteristics and HWA infestation levels as independent variables affecting radial growth during an 11-year period.

Study design and methods

Study area

Delaware Water Gap National Recreation Area (DEWA) occupies approximately 27,800 ha along the Delaware River in northeastern Pennsylvania and northwestern New Jersey. Forest stands are primarily dominated by eastern deciduous species with pure hemlock stands occupying about 5% of the landscape, typically in patches within isolated ravines along the Delaware River (Eschtruth et al. 2006). In the mixed-stands, hemlock can occupy 30–70% of the basal area (Mahan et al. 2004). HWA infestations were first detected in the park in 1989 (Evans 1995) and declines in hemlock health were evident in 1992.

From 1993 to 1995, a system of permanent plots was established in five distinct hemlock stands: Adams Creek (AC), Grey Towers (GT), Toms Creek (TC), Mount Minsi (MM) and Van Campens Creek, (VC). In these stands there was no evidence of HWA infestation prior to plot establishment. In 1998, an additional set of permanent plots was added at Donkeys Corner (DC), which was known to have HWA infestation in 1993. Sites selected were representative of the variation in slope aspect, slope position, elevation, relative stocking, and species composition typical of hemlock stands in DEWA.

Within each stand, plots were randomly located and consisted of 10 permanently tagged hemlocks that were selected along a 6 m wide variable length transect (mean length = 32 m) measured from the outer edge of tree 1 to the outer edge of tree 10. Each plot traversed along the contour to maintain elevation, slope and aspect consistency within the plot. The first 10 hemlocks greater than 2 cm were selected as plot trees with no more than two of the 10 trees smaller than 10 cm. Plot tree crown positions were classified as dominant, co-dominant, intermediate, or overtopped (Smith et al. 1997). The majority of plot trees were in the dominant or co-dominant crown class. A total of 81 plots were established.

Field measurements

From 1993 to 2003, the following observations were recorded annually for the sample trees in each stand: live crown ratio (LCR) (ratio of live crown to total height), crown density (an estimate of the fullness of the crown, based on the amount of skylight blocked by leaves, branches, bole, and fruits), crown dieback (percent of branches with newly dead twigs in the live crown), and foliage transparency (relative amount of light that passes through a tree live crown), (all definitions from Montgomery et al. 2006). All crown ratings were assessed to the nearest 5% compared to an ideal, healthy tree, consistent with Forest Health Monitoring Visual Crown Rating methodologies (Schomaker et al. 2007).

Trees were also assigned a vigor rating category as follows: H = healthy (tree appears healthy with less

Table 1 (a) U.S. Department of Agriculture Forest Service Crown Condition Rating Guide (Millers et al. 1992) tree vigor indicators and classification thresholds; (b) Decision rules for determining the Visual Crown Rating (VCR) (modified from Bonneau et al. 1999)

	Condition 1 (%)	Condition 2 (%)	Condition 3 (%)
(a)			
Live crown ratio	>40	20–35	5–15
Crown density	>55	25–50	5–20
Dieback	≤5	10–25	≥30
Foliar transparency	≤45	50–70	≥75
(b)			
Good	All factors are condition 1, or only one condition 2 and no condition 3		
Average	All factors are either condition 1 or 2; none are condition 3		
Poor	One or all factors are condition 3		

than 10% branch or twig mortality or foliage discoloration), LD = light decline (branch or twig mortality, or foliage discoloration on 10–25% of crown), MD = Moderate decline (branch or twig mortality or foliage discoloration on 26–50% of crown), SD = severe decline (branch or twig mortality or foliage discoloration on more than 50% of crown), or DN = dead natural (no live foliage). During 1998–2001, some logistical issues in field sampling limited measurements to sub-sampling different plot trees each year.

From 1996 to 2003, an HWA infestation index was estimated each June for a subsample of plots. The proportion of branch terminals with HWA ovisacs, from permanently marked lower branches of three trees, was averaged to produce the plot-level HWA infestation index (PHWA) (Evans 1996; Costa 2006). Because all plots had been infested with HWA before 2003, the number of years each plot was exposed to HWA (up to 2003) was calculated as: 2003 − the first year for which plot-level infestation was greater than zero. In addition, the annual plot-level infestation averages were summed for 1996–2003 to derive a cumulative infestation index (%) (CHWA). Site variables measured at each plot included slope aspect (cardinal direction), percent slope, and soil type (loam or rocky). Percent hemlock basal area was also determined.

In November 2003, increment cores were collected from a subset of 147 trees that represented a range of site conditions and HWA-infestation histories. Of these, 29 trees also had measurements of HWA branch infestation. For most trees, two cores were extracted at 1.37 m above the ground (breast height or bh). Cores were air-dried and sanded. Ring widths were measured to the nearest 0.001 mm using a dissecting microscope in conjunction with J2X software (VoorTech Consulting 2000) to organize the data. Ring width series were averaged to yield a single growth chronology for each sample tree.

Analyses

Because percent dieback and foliage transparency were strongly correlated ($r = 0.73$, $P < 0.0001$), a modified adjusted ZB-index (proposed by Zarnoch and others as cited in Coulston et al. 2005) was used to minimize multicollinearity. The formula was modified by a using a multiplier of 100 to make the outcome the same order of magnitude as the other crown descriptors in this study.

$$ZB_{adj} = 100 * [1 - (1 - (T - 15)/100)(1 - D/100)] \quad \text{where } T \geq 15\%$$

$$ZB_{adj} = D \quad \text{where } T < 15\ \%$$

Where:

ZB_{adj} = adjusted ZB-index ($0 \leq ZB_{adj} \leq 100$)
T = percent foliar transparency ($0 \leq T \leq 100$)
D = percent dieback ($0 \leq D \leq 100$)

Theoretically, this index represents the amount by which the foliage of a tree is reduced relative to an ideal, fully foliated tree having the same live crown ratio, and crown density. A threshold of 25 was selected to indicate trees that had poor or unhealthy crowns. Thus, a tree with $ZB_{adj} = 25$ would have 75% (100 − 25 = 75) of the foliage that an ideal, fully foliated tree would have.

Another composite crown condition index was calculated by integrating LCR, crown density, dieback, and foliar transparency. The USFS Crown Condition Rating Guide (CCRG) developed by Millers et al. (1992), was used to establish appropriate ranges for the three conditions of each crown variable (Table 1a). Trees were then classified into a Visual Crown Rating (VCR) as good, average, or poor, using the modified decision rules cited by Bonneau et al. (1999) found in Table 1b.

Tree age and tree diameter at breast height (dbh) were derived from each tree's ring-width chronology. To account for the effect of annual climatic variation on tree growth and vigor, annual dormant season (November–March) temperature, annual minimum temperatures, and growing season (May–September) precipitation averages from the Stroudsburg, PA weather station were included as independent variables (NCDC 2006).

Model development

Annual tree-ring date assignments were validated using the COFECHA program (Grissino-Mayer et al. 1997). This program estimates a master chronology for each site by cross-dating ring-width patterns of 50-year segments lagged successively by 25 years. Individual series (increment cores from individual trees) that did not satisfactorily correlate to the Master chronology (e.g., $r < 0.3281$, 99% confidence level) for years 1980–2003 for each of the five study sites were omitted from further analyses.

The sample trees represented a range of ages, sizes and crown positions. Tree ages ranged from 40 to 240 years (mean = 103, standard deviation = 101), diameters ranged from 5 to 61 cm (mean = 26.7, standard deviation 12), and crown class distributions included 80 codominant, 40 intermediate and 18 overtopped trees. Because ring-width measurements are not independent and decrease with increasing age or tree size, radial growth trends were removed from each tree-ring series using the ARSTAN program (Cook and Krusic 2005). This program produces chronologies by detrending and indexing (standardizing) each series to yield a series of independent data points with a mean of one and equal variance. The detrending process does not remove short-term, high frequency trends, such as a growth response to HWA feeding or drought. The output of the program is a dimensionless ring width index (RWI) for each tree and each year, obtained by dividing the actual value by the expected value from the fitted model. A RWI = 1 represents average growth, while values > or <1 indicate above- and below-average growth, respectively. A modified negative exponential curve fitted to the raw ring-width series had the best "fit" to the data and so was used as the detrending model for the RWI.

Based on observations that hemlock mortality may occur as quickly as four years after infestation (McClure 1991), a decline threshold was defined as three consecutive years with below average growth (RWI < 1). This binomial (1 = decline; 0 = no-decline) decline value was calculated as the response variable for each tree for years 1993–2003.

A multiple logistic response function was developed to predict the likelihood of tree decline from 1996 to 2003, using site conditions, HWA infestation (PHWA and CHWA), tree age, canopy position and visual crown health characteristics as predictor variables. Because the response variable is binary, the shape of the response function is frequently curvilinear. Nonlinear regression models are appropriate for analyzing data from observational studies where the predictor variables may be both quantitative and qualitative (Neter et al. 1996).

Each variable was first evaluated individually using the method of maximum likelihood to estimate the parameters of the multiple logistic response function (Proc Logistic, SAS V. 9.1 2004). Those with statistically significant maximum likelihood estimates (MLE, $P < 0.05$) were then evaluated together using logistic regression with backward selection (P to enter and P to stay = 0.10). In this analysis, regression coefficients were derived from MLEs that were exponentiated and expressed as odds-ratios that a unit-change in the value of an independent variable was associated with hemlock decline. The Wald statistic tested the significance of individual independent variables, and the Hosmer-Lemeshow test determined the goodness-of-fit between the observed and predicted values for the overall model (SAS 2004).

Generalized linear models analysis (Proc GLM, SAS Institute Inc. 2004) was used to assess the annual variability of crown and tree measurements as a function of site, crown class, and decline status as well as the interactions of site and crown class with decline status. Multiple comparison and means separation were performed using Tukey's HSD.

Results

Crown variables

For every crown metric, variations in mean values by stand, crown class, and decline status were statistically significant, as was the interaction of stand x decline. Trees in decline had lower crown density and LCR, and greater transparency, dieback, ZB_{adj} values, as well as greater age and diameters ($P < 0.05$, see Table 2). However, within crown classes, only tree age was significantly different by decline status.

Live crown ratio showed the smallest amount of variation over the 11-year time period considered, and within stands, there were no significant differences for mean LCR by year (Fig. 1a). Crown density exhibited a decrease as early as 1994 for four study sites (DC had not yet been established), a recovery in 1995, followed by a decreasing trend from 1996 to 2002. By 2003, crown density for VC and TC had more or less returned to pre-infestation values (Fig. 1b). Dieback increased dramatically after 2000 (Fig. 1c), and both crown transparency and ZB_{adj} increased quite steadily after 1998 (Fig. 1d and e). Mean values of dieback, crown transparency, and ZB_{adj} in 2003 were 4–6 times greater than values in 1993.

Among stands, VC showed the least impacts of HWA infestation in crown density, live crown ratio, and ZB_{adj} trends, while site DC showed the greatest relative amount of dieback and crown transparency. For example, while mean dieback was <15% at all

Table 2 Least square means (SE) for crown and tree variables at five stands in DEWA, 1996–2003, by decline status

	Decline = 1			Decline = 0		
	N	LS mean	SE	*N*	LS mean	SE
Crown density (%)	412	35.81	0.54	295	38.22	0.62
Dieback (%)	291	21.10	1.14	163	13.37	1.01
Live crown ratio (%)	413	55.59	0.96	295	58.53	1.13
Transparency (%)	405	33.84	0.75	294	27.79	0.69
ZB_{adj}	289	38.39	1.34	163	28.75	1.44
Tree age (years)	668	104.17	1.22	544	94.22	1.32
Tree diameter (cm)	660	27.89	0.47	544	24.74	0.52

Tree decline is defined as three consecutive years with radial growth below average. Decline = 1 for $year_n$ if RWI < 1.0 for $year_n$, $year_{n-1}$, and $year_{n-2}$. Means of all variables were statistically significant different ($P < 0.05$) by decline status

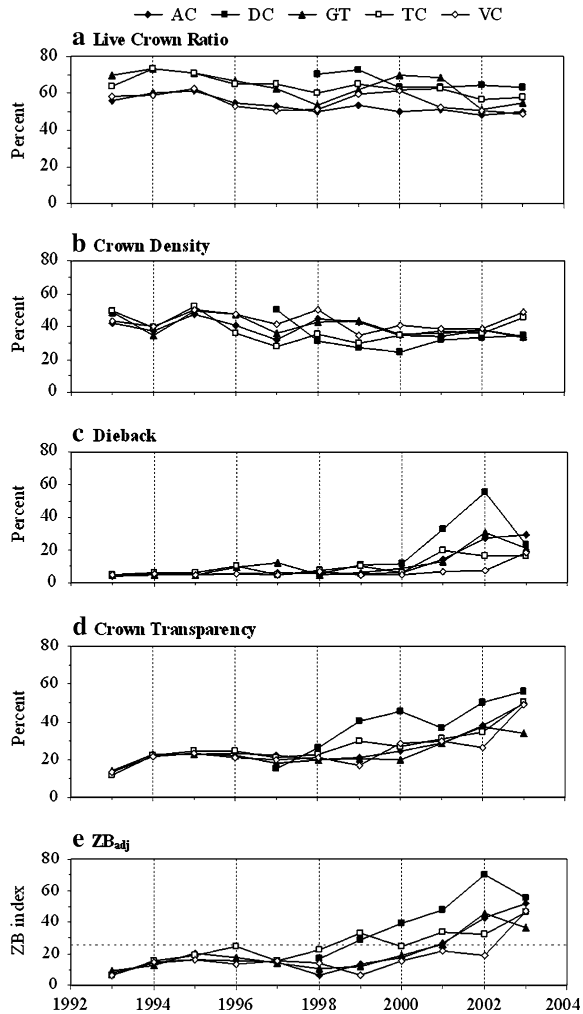

Fig. 1 Annual means for (**a**) live crown ratio (LCR), (**b**) crown density, (**c**) dieback, (**d**) crown transparency, and (**e**) the calculated ZB_{adj} index at five sites in the DEWA, 1993–2003

stands during 1993–2000, dieback increased to 55% at DC in 2002, but dieback remained below 10% at VC through 2003. A similar temporal pattern was exhibited for the ZB_{adj} variable.

For trees in decline, codominant trees displayed significantly higher values of all crown variables except LCR compared to intermediate and overtopped trees. Overtopped trees in decline had a greater LCR than trees in the other crown classes. Overtopped trees also tended to be classified as in decline at significantly lower HWA infestation levels than either intermediate or codominant trees. For all crown classes, the means for dieback and transparency of trees in decline were considerably lower than the 60% thresholds cited by Mayer et al. (2002) for onset of significant mortality (Table 2).

Radial growth and decline

Ages of oldest hemlocks ranged from 82 years in DC to more than 224 years at GT. The raw ring-width series displayed the typical biological pattern of decreasing radial growth trends at all stands (Fig. 2a). Stands GT and TC always exhibited below average growth (RWI < 1), and all stands showed below average growth after 1997 (Fig. 2b). Between 1993 and 2003, the percentage of trees in decline increased at an average annual rate of 3% for all stands (Fig. 2c), although within stands, the mean percentage of trees in decline in any given year did not differ. Stands GT, VC, and TC exhibited spikes in the percentage of trees in decline in 1988 (before any HWA was detected), and again in 1994 and 1999, paralleling trends for crown density. Decline curves for AC and DC showed a consistent increasing trend until an abrupt increase at DC after 1995, and at AC after 1997 (Fig. 2c). At DC, the percentage of trees in decline increased from 41% in 1998 to 96% in 2001. The percentage of trees in decline, from 1993 to 2003, closely paralleled the curve of increasing mean ZB_{adj} (and thus dieback and transparency; see Figs. 1f and 2c).

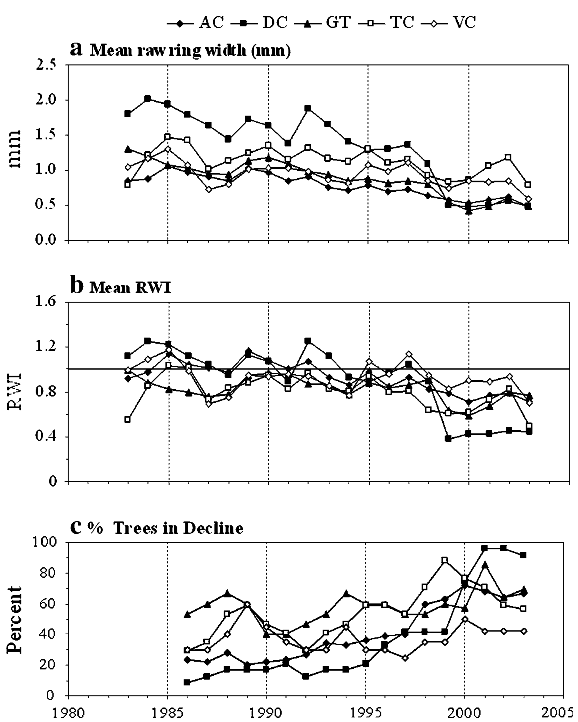

Fig. 2 (**a**) Mean raw ring-width (mm); (**b**) mean ring-width index (RWI); (**c**) percent of trees in decline (defined as three consecutive years with RWI < 1), at five sites in the DEWA, 1983–2003

Logistic regression

Fifteen site, tree and crown variables were statistically significant when considered individually in the logistic model (Table 3a), and five (LCR, crown density, tree diameter, ZB_{adj}, and plot HWA infestation level), were statistically significant based on maximum likelihood

Table 3 Maximum likelihood estimates and odds ratios from multiple logistic regression predicting hemlock decline during 1996–2003, as a function of stand, tree, crown, and site variables

	MLE	SE	*P*	Odds ratio
(a) Individual runs of independent variables				
Stand TC vs. VC	0.512	0.155	0.00	3.73
Crown class (I vs. OT)	0.312	0.093	0.001	2.10
Aspect N vs. W	−0.634	0.132	<0.0001	0.68
Aspect S vs. W	0.789	0.213	0.000	2.81
Transparency	0.034	0.006	<0.0001	1.03
Diameter	0.023	0.005	<0.0001	1.02
Live crown ratio	−0.007	0.004	0.070	0.99
Dieback	0.031	0.007	<0.0001	1.03
Crown density	−0.021	0.007	0.004	0.98
ZB_{adj}	0.023	0.005	<0.0001	1.02
Transparency	0.034	0.006	<0.0001	1.03
Tree age	0.009	0.002	<0.0001	1.01
Time of exposure	0.158	0.026	<0.0001	1.17
PHWA[a]	0.008	0.004	0.039	1.01
CHWA[b]	0.003	0.084	0.009	1.003
(b) Overall model				
Live crown ratio	−0.019	0.007	0.016	0.98
Crown density	−0.027	0.014	0.004	0.97
Diameter (dbh)	0.029	0.013	0.029	1.01
ZB_{adj}	0.015	0.007	0.031	1.02
PHWA[a]	0.080	0.025	0.002	1.08

(a) Shows results of individual runs for each statistically significant variable. In (b), five of the variables found significant in (a). were also significant when tested in the complete model using logistic regression with backward selection

[a] Plot infestation index (%)

[b] Cumulative plot infestation index (%)

estimates of the complete model (Table 3b). Other plot-level variables (percent slope, soil type, percent hemlock basal area) showed no significant relationship with the onset of tree decline in the final model. In addition, neither temperature nor precipitation was associated with the likelihood of tree decline. A *t*-test comparing mean dormant season temperature and growing season precipitation values of the 11-year plot monitoring period to the previous 43-year period (1949–1992) showed no significant differences between the two periods for either comparison ($t = -0.894$, $P = 0.194$; $t = 1.097$, $P = 0.146$ for temperature and precipitation, respectively).

Eastern hemlock trees on south facing slopes were 2.8 times more likely to exhibit growth decline than those on west facing slopes. Whereas, trees on north facing slopes were 32% less likely to exhibit growth decline than those on west facing slopes. There was no difference in growth decline between east and west facing slopes. At the stand level, trees at TC were 3.7 times more likely to be in decline than trees at VC for the period 1996–2003 (Table 3a).

Crown class also showed a strong correlation with decline trends. Although no differences were detected between codominant and overtopped trees, intermediate class trees were 2.1 times more likely to undergo decline than overtopped trees. The odds relationship was not linear with respect to time. For years 1993–1997 (excludes site DC), before significant infestation, there was no significant relationship between crown class and tree decline, which is consistent with the overall relationship between exposure time and decline probability. When time of exposure to HWA was considered individually in the model, every additional year of exposure was associated with a 17% increase in the odds of decline.

Based on the 5 significant variables included in the complete model, the best fit model for estimating the odds of a hemlock being classified as in decline is:

$$P = \frac{e^{[0.944-0.019(\mathrm{LCR})-0.027(\mathrm{CD})+0.029(\mathrm{DBH})+0.015(\mathrm{ZB})+0.08(\mathrm{PHWA})]}}{1 + e^{[0.944-0.019(\mathrm{LCR})-0.027(\mathrm{CD})+0.029(\mathrm{DBH})+0.0153(\mathrm{ZB})+0.08(\mathrm{PHWA})]}}$$

where P is the probability of a tree classified as being in decline and CD is crown density. The logistic response function was found to be appropriate for the data according to the Hosmer and Lemeshow goodness of fit test ($\chi^2 = 12.26$, $P = 0.145$). Although the adjusted R^2 for the model was only 21%, the model correctly classified 237 of 360 "events" (66%) between 1996 and 2003 (170 decline events and 69 no-decline events). Model sensitivity and specificity, the probabilities of detecting true decline and no-decline events, were 0.80 and 0.47, respectively.

This model indicates the following:

- Every 1% decrease in live crown ratio (LCR) was associated with a 2% increase in the likelihood that a tree will be classified as in decline.
- Every 1% decrease in crown density (CD) was associated with a 3% increase in the likelihood that a tree will be classified as in decline.
- Every 1 cm increase in tree diameter (DBH) was associated with a 1% increase in the likelihood that a tree will be classified as in decline.
- Every one unit increase in $\mathrm{ZB}_{\mathrm{adj}}$ (ZB) was associated with a 2% increase in the likelihood that a tree will be classified as in decline.
- Every 1% increase in mean percent HWA plot infestation level (PHWA) was associated with an 8% increase in the likelihood that a tree will be classified in decline.

Discussion

Site and tree variables

Plot HWA infestation level was the best predictor of the onset of hemlock growth decline, whereas tree crown variables were more likely to reliably predict the degree of hemlock decline after infestation. Although no significant relationship was found between decline and crown class in the final model, when tested individually, intermediate-class trees showed a higher likelihood of decline than overtopped trees. Crown structure and related attributes may contribute to the persistence of overtopped trees during at least initial HWA infestation. For example, compared to red spruce, hemlocks capture a greater proportion of two-dimensional growing space because they tend to have a lower and wider crown (Kenefic and Seymour 2002). Due to high shade tolerance, hemlock can retain foliage on its lower branches (Bonneau et al. 1999), except when in direct physical competition with another hemlock crown. It can survive and grow successfully in the understory, even in two or more subcanopy layers (Rogers 1978; Fajvan and Seymour 1993).

In our study, mean LCR of overtopped trees was significantly greater than means for dominant and intermediate trees. While there was some evidence that intermediate trees were more vulnerable to decline, there were no differences in likelihood of decline between codominant and overtopped trees. This finding demonstrates the interaction between tree vigor, crown size and HWA ecology. Codominant trees receive full light from above and some side light to their crowns without being considered "crowded" (Smith et al. 1997). Under favorable growing season conditions, codominant trees can probably offset some growth loss from light HWA infestation by maximizing flushes of new shoot growth. Intermediate trees are shorter than codominants, receive little light from above and are very crowded on the sides. Stem biomass is less than codominant trees however, shorter live crowns means new annual growth is probably barely sufficient to support current stem maintenance. Therefore, intermediate trees cannot afford to lose foliage during even a light HWA infestation because they already have insufficient carbohydrate reserves. Alternatively, even though overtopped hemlocks are receiving no direct light, they can develop very long, wide live crowns to utilize all available low light, provided there is no competition from the sides. Overtopped trees are smaller in diameter, have less stem biomass to support and are growing slower than codominants and intermediates. With lower energy demands, overtopped trees may tolerate HWA feeding (and other stress) longer than intermediates.

As HWA densities increase over time, overtopped trees will likely be impacted at a faster rate than codominants. Physiologically, hemlocks can fix carbon in the winter as long as temperatures are above −5°C (Hadley and Schedlbauer 2002). About 10–30% of hemlock's annual carbon uptake can occur during winter (Hadley 2000a; Catovsky et al. 2002) but carbon fixation rates of understory hemlocks are always lower than upper canopy; late spring is probably the time of their greatest photosynthesis (Hadley 2000b). Thus, HWA's winter feeding habit could severely impact winter carbohydrate storage in hemlock, especially in the understory, which results in decreased foliage and wood production in the subsequent growing season.

Although the VCR variable did not enter the final model, several of its component metrics (i.e., LCR, crown density, and ZB_{adj}) did. The failure of VCR to account for decline is probably due to the condition thresholds for each crown descriptor that are collectively used to classify tree health. A comparison of these condition thresholds (Table 1) with the mean values of crown indicators for trees in decline (Table 2), resulted in classifications of either condition 1 or condition 2. Using these ranges and the decision rules proposed, 204 tree-year combinations were classified as "good," 352 as "average," and only 8 as "poor."

Crown condition has been linked to tree survival and mortality (Dobbertin 2005), shoot and root growth (Renaud and Mauffette 1991; Straw et al. 2000; Smith and Schowalter 2001), carbon and nutrient allocation (Liu and Tyree 1997), and symbiotic relationships in the root zone (Gehring and Whitman 1995). Individually, dieback, transparency, and ZB_{adj} accounted for the largest proportion of variation in decline ratings of all variables (6.7%, 6.1%, and 6.3%, respectively). Crown density exhibited early fluctuations (Fig. 2b), which may be linked to the observation that hemlock's initial response to infestation is a new growth flush (Mayer et al. 2002). Alternatively, LCR showed much less variation over the study period compared to other crown variables (Fig. 1). The R^2 value for LCR was only 1.0%, and its odds ratio was only 0.98. LCR is a measurement that is consistently repeatable among annual observers and is only dependent on foliage presence. In addition, trees with low HWA populations tend to have a larger percentage of nymphs in the upper crown; heavily infested trees have more nymphs in the lower crown (Evans and Gregoire 2007). Therefore, because most of our study trees had low to moderate infestation levels, crown length and hence LCR would not have changed much over the measurement period.

Site factors

The extent to which the interaction of other insects, site conditions and stand structure affect hemlock's vulnerability to HWA or vice-versa is still unclear. Scientific and empirical evidence indicates that while healthy hemlocks are not less susceptible to HWA infestation, they do have a better chance of surviving longer (i.e., less vulnerable) than stressed trees (e.g., crowded conditions, other insect pests), and possibly recovering (Orwig and Foster 1998). Average plot-level HWA infestation was the only site-specific factor that yielded a significant relationship with the onset of tree decline as calculated in the final model of this study. Because 90% of the sample trees were found in loam soils, there were no correlations between percent slope and soil type. Plots were distributed across all slopes represented in the study area except the steepest ($\geq$70%), which had about ten sample trees.

Aspect showed a significant relationship with decline when considered individually, but not in the final model. Eastern hemlock's range is restricted to cool humid climates in areas with well-drained moist soils (Godman and Lancaster 1990). Many expected ecological impacts of adelgid-induced mortality arise from hemlock's importance to temperature-sensitive areas such as headwater streams, deep ravines and stream sides (Snyder et al. 2005). In our study, trees on north and west-facing slopes were less likely to show decline that those on south-facing slopes. However, site preferences vary with region; in the southern portion of its natural range, hemlocks are commonly restricted to north and east-facing slopes, coves, or cool, moist valleys (Godman and Lancaster 1990). In New England, closer to its northern limit, its distribution is often bimodal: abundant in mesophytic ravines and stream draws, and also on more xerophytic exposed slopes, but rare on intermediate sites. Russell (1979) identified distinct growth and morphological traits associated with each habitat type, and Bonneau (1997), found that stands on cold, moist, north-northeast aspects were generally healthier than stands on drier, more exposed locations.

DEWA is located approximately in the middle of hemlock's range where site preferences are less specific and hemlock occupies a wide range of aspects and slopes among stands >100 years old (Kavanagh and Kellman 1986). Indeed, our sample trees were fairly evenly distributed among slope aspects. Although mean annual RWIs (pre-infestation, 1983–1992) were significantly less on south-facing slopes ($P < 0.05$), the magnitudes of differences were relatively small (RWI means: W = 1.07, N = 0.99, E = 0.99, S = 0.89), and the amount of variation of the response variable accounted for by aspect was only 2.2%. These results generally reinforce other studies that either failed to find a significant correlation between site variables and the onset of hemlock infestation, decline and/or mortality (Orwig and Foster 1998; Eschtruth et al. 2006), or did find a strong correlation but only a small amount of the total variation in tree response was accounted for (Royle and Lathrop 2000).

Vulnerablility of hemlock forests to HWA

Many forest ecosystems are currently experiencing unprecedented levels of disturbance from introduced pathogens and pests (Liebhold et al. 1995). These introductions represent a major environmental problem that is likely to escalate in the future (Muzika and Liebhold 1997). HWA is a serious threat to the future health and existence of eastern hemlock trees and their associated ecosystems. The direct effects of HWA are hemlock decline and mortality. Indirect effects include changes in vegetation species composition and structure (Kizlinski et al. 2002), such as increased non-native plant populations (Eschtruth et al. 2006), changes in wildlife habitat (Ross et al. 2004), altered decomposition and nutrient cycling rates (Jenkins et al. 1999; Stadler et al. 2005), and changes in fish and benthic macroinvertebrate communities from altered temperature regimes in headwater streams (Snyder et al. 2001, Snyder et al. 2005; Ross et al. 2003). There are also considerable aesthetic and economic impacts, including the management of dead and dying hazardous trees (Evans 2004).

This study predicted the odds of hemlock radial growth decline based on the relationship of crown condition and infestation by HWA. We used tree-ring chronologies of eastern hemlock to develop a binomial decline index based on three consecutive years of below average growth. We then modeled hemlock decline as a function of an extensive array of tree, crown, and site variables that were collected over an 11-year period. Some site-related variables such as site-location and aspect were significantly related to decline probabilities when considered individually. However, the total proportion of response variable variance accounted for was low, and these variables did not enter the final model. Crown variables such as live crown ratio, crown density, and the modified ZB_{adj} index, a combination of transparency and dieback, had the most explanatory power, both individually, and in the final model, and were relatively accurate predictors of hemlock decline. Of the site variables, only the average percentage of branches with HWA present entered into the final model.

The logistic model was relatively accurate in predicting tree decline using crown and tree characteristics although, its overall explanatory power was modest ($R^2 = 21\%$). The relatively poor fit between the logistic model and hemlock decline is partly attributable to the large number of empty cells in the data matrix. The final model incorporated 360 of the 1,144 possible observations. The rest of the observations were deleted due to missing values for one or more of the independent variables.

Even with the limitations of the current data set, long-term repeated measurements of ecosystem structure are critical to develop an understanding of temporal changes that result from invasive pests such as HWA. Understanding the changes in ecosystem composition, structure, and function that result from invasions is a developing science. Our findings indicate that there is a predictable pattern of hemlock vulnerability at light and moderate HWA infestation. As HWA populations build and create more physiological stress to trees, hemlock's vulnerability becomes more ubiquitous.

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